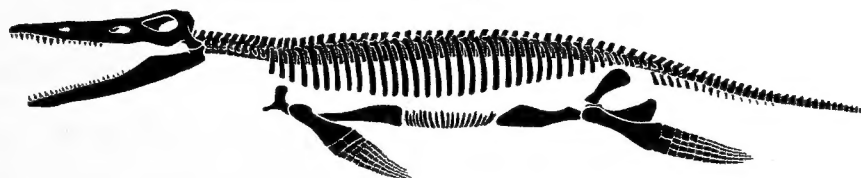


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AN ECOMORPHOLOGICAL ANALYSIS OF NATIVE AND INTRODUCED POPULATIONS OF THE ENDEMIC LIZARD *ANOLIS MAYNARDI* OF THE CAYMAN ISLANDS

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ABSTRACT. *Anolis maynardi* is an endemic anole from Little Cayman (Cayman Islands) that is characterized by an extremely elongated rostrum in males. In the 1980s, this species was discovered on the nearby island of Cayman Brac where it was likely introduced. Despite its unusual morphology and endemic status, little is known about the abundance, ecology, or natural history of this species. Our data suggest that animals from the two islands are distinct in their morphology, performance, and ecology: Cayman Brac lizards utilize more open habitats, have relatively longer limbs and shorter heads, but higher bite forces on average. Moreover, a distinct sexual dimorphism is present in both populations in which males have relatively larger heads and longer limbs than females.

INTRODUCTION

Anolis maynardi is endemic to the small (28 km²) island of Little Cayman. Typical of other members of the *carolinensis* species group, and of “trunk-crown” ecomorphs in

general (Williams, 1983; Losos, 2009), this primarily arboreal species is green with the ability to change color to brown, and has relatively short legs and large toepads. *Anolis maynardi* is notable in one respect, however: it has an enormously elongated, pincer-like rostrum that is equaled in anoles only by *Anolis longiceps* of Navassa Island, to which *A. maynardi* may be closely related (Glor *et al.*, 2005). Why this unusual rostral morphology has evolved in these species is unknown.

Indeed, almost nothing is known about the natural history of *A. maynardi*. Chapman Grant in “The Herpetology of the Cayman

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Islands" (1940) stated that "It is stealthy in movements, apparently stupid...a tree lizard occasionally found on the ground; when in a tree it faces upwards showing that its prey is aboreal (sic)..." Seidel and Franz (1994) found that "it appears to be extremely arboreal and escapes to the upper portions of trees or buildings when pursued...the forceps-shaped snout suggests some unique feeding adaptation." Henderson and Powell (2009) also report that this species is usually arboreal and occurs on a wide variety of perches, including roadside bushes, cactus, and agave. Losos and de Queiroz (1997) recorded males perching on average 2.5 m above the ground on perches 11 cm in diameter.

The distribution of *A. maynardi* on Little Cayman has also received little attention. Grant (1940) reported that this species may be more common in thicker vegetation and on the northern side of the island. Although the equally small island of Cayman Brac lies only 7.5 km distant from Little Cayman, *A. maynardi* never colonized this island. However, Franz *et al.* (1987) discovered the species in the vicinity of the airstrip on Cayman Brac, and in 1991, this was the only location on the island where the species was detected (Losos *et al.*, 1993). No further reports of the fate of this introduced population exist in the literature.

Given that so little is known about the natural history of this morphologically unusual species, we visited Little Cayman and Cayman Brac in April 2009 to collect basic data on the occurrence and distribution of the species in its native habitat on Little Cayman, provide an estimate of its abundance in optimal habitat patches, and compare native and introduced populations with respect to morphology, ecology, and performance. Finally, we also examined differences between the sexes in morphology,

performance, and ecology to better understand the potential role of the unique elongated rostrum in males.

MATERIALS AND METHODS

Field sites

Data were collected on Little Cayman 5–10 April 2009 and on Cayman Brac 10–15 April 2009. Sites throughout the island of Little Cayman were surveyed for the presence of *A. maynardi* to estimate its distribution across the island. Global positioning system coordinates were recorded at all localities where animals were observed.

Temperature

Animals were caught by noose or by hand and body temperature was measured for all lizards that were caught immediately using a quick-reading thermometer (Miller and Weber, Inc.). The air temperature was then measured at the site the lizard was first observed.

Morphometrics

Animals were taken back to the field laboratory where they were weighed (Scout Pro balance) and measured using digital calipers (Mitutoyo). For each individual, we measured the following: head length, from the back of the parietal to the tip of the snout; head width, the width at the widest point of the head; head depth, the depth at the tallest part of the head; lower jaw length, the length of the lower jaw from the back of the retroarticular process to the tip of the lower jaw; jaw out-lever, the distance from the quadrate to the tip of the lower jaw; snout length, the distance from the back of the jugal to the tip of the lower jaw; interlimb length, measured between the

anterior edge of the sternum and the posterior edge of the pelvis; body width at the widest point; body depth at the shoulder; tail length; femur length; tibia length, metatarsal length; the length of the longest toe on the hind foot; humerus length; radius length; metacarpal length; and the length of the longest toe on the front foot. All measurements were taken on the left side of the animal and by the same observer. On the basis of these measures, four additional variables were calculated: the in-lever for jaw opening by subtracting the distance from the quadrate to the tip of the jaw from lower jaw length; the in-lever for jaw closing by subtracting the distance from the jugal to the jaw tip from the distance from the quadrate to the jaw tip; hind-limb length, the sum of all hind-limb segments; and forelimb length, the sum of all forelimb segments.

Bite force

Bite force capacity was measured using an isometric Kistler force transducer (type 9203) mounted on a purpose-built holder and connected to a charge amplifier (type 5995; for details of the setup see Herrel et al., 1999). Lizards were induced to bite the transducer five times, and the highest bite force recorded was used as an estimate of an individual's maximal bite performance.

Sprint speed

Sprint speeds were quantified for individuals on Cayman Brac only. Animals were filmed running up a 2-m-long dowel of 3 cm in diameter and placed at 45° using a portable Redlake Motion Meter (IDT, Tallahassee, Florida) camera set at 250 Hz. Three trials were recorded for each individual. In between trials, lizards were put in bags placed in half-sun, half-shaded conditions, allowing lizards to select their preferred temperatures. Video clips were streamed to a Sony HDV recorder

(GV HD700) and recorded on tape. Subsequently, clips were digitally transferred to the computer, cropped, and exported as jpg sequences. The snout tip was digitized on all sequences using Didge (A. Cullum, Creighton University, Omaha, Nebraska) and scaled coordinates were exported to Excel. Raw displacement profiles were calculated and smoothed using a fourth-order zero phase shift butterworth filter with cut-off frequency set at 30 Hz (Winter, 2004). Velocities were calculated through numerical differentiation of the smoothed displacement profile. Finally, the average speed over 20-cm intervals was calculated. The fastest 20-cm interval of the three trials was then considered an individual's maximal sprint speed. All trials were scored as good or bad and only trials that were scored as being "good" were retained for analysis.

Habitat use

For every lizard caught, the following habitat characteristics were measured: perch height; perch diameter; distance to the nearest perch, defined as any part of the structural habitat upon which an animal could perch; and the diameter of this nearest perch. For each individual found sleeping during night surveys we recorded the perch height, perch diameter, and the type of substrate on which animals were sleeping.

Population density estimates

We searched a strip of habitat composed of sea grape (*Coccoloba uvifera*) trees between a coastal road and the sea on Little Cayman (extending 19.6744132°N, 80.0475083°W to 19.6732964°N, 80.0454986°W) for sleeping *A. maynardi*. Individuals were marked with nontoxic paint markers to allow identification. On nights 2 and 3, we failed to recapture any previously marked

lizards, but on night 4, we recaptured two individuals that had been previously marked. To make a preliminary population density estimate, we treated the first three nights as a single sampling session and the fourth night as a second sample and calculated population size using the Lincoln–Petersen method.

Analyses

All morphological and habitat use data were \log_{10} -transformed before analysis to meet assumptions of normality and homoscedasticity. To test for differences between sexes and populations (Little Cayman versus Cayman Brac), we first tested whether there were significant differences in body size using a two-way analysis of variance (ANOVA). Next, we tested for differences in head dimensions and bite forces using a multivariate analysis of covariance (MANCOVA) with snout–vent length as covariate. Similarly, we tested for differences in body and limb dimensions using a MANCOVA with snout–vent length as a covariate. Differences in habitat use and sleep site characteristics were tested using multivariate ANOVAs. In all cases, nonsignificant interaction effects were removed from our final model. An ANOVA was used to test for differences in sprint speed between the sexes. All analyses were performed in SPSS (v. 15.0).

RESULTS

Distribution and population density on Little Cayman

We surveyed sites across the entire island covering all vegetation types to investigate the presence and distribution of *A. maynardi* on Little Cayman. Animals were observed in all vegetation types, but densities appeared to differ considerably between the vegetation types; animals were most abundant in sea grape-dominated hemisclerophyllous ever-

green shrubland (Burton, 2008) and least abundant in mangroves. On the basis of our pilot mark–recapture study, we estimated a population density of 314 individuals in the surveyed patch of sea grape habitat. This leads to a density estimate of 0.06 animals per square meter.

Body size

Males were larger on average than females on both islands ($F_{1,62} = 499.89$; $P < 0.001$), but lizards from the two islands did not differ in size ($F_{1,62} = 0.16$; $P = 0.69$), nor was there an interaction between sex and island ($F_{1,62} = 1.54$; $P = 0.22$; Table 1).

Head dimensions and bite force

Both sexes (Wilks' lambda = 0.52; $F_{9,53} = 2.54$; $P < 0.001$) and islands (Wilks' lambda = 0.43; $F_{9,53} = 7.89$; $P < 0.001$) differed with respect to head dimensions and bite force, and the interaction term was marginally nonsignificant (Wilks' lambda = 0.74; $F_{9,53} = 2.06$; $P = 0.05$). Subsequent univariate analyses of covariance testing for differences in intercept indicated significant differences between sexes in head length ($F_{1,61} = 27.90$; $P < 0.001$), head width ($F_{1,61} = 5.61$; $P = 0.02$), lower jaw length ($F_{1,61} = 39.84$; $P < 0.001$), the distance from the quadrate to the tip of the snout ($F_{1,61} = 23.99$; $P < 0.001$), and snout length ($F_{1,61} = 33.96$; $P < 0.001$), with males having relatively longer and wider heads than females (Fig. 1; Table 1). No differences in slopes were observed. Animals from Little Cayman had longer and wider heads, but lower bite force, than animals from Cayman Brac for a given body size: head length ($F_{1,61} = 13.71$; $P < 0.001$), head width ($F_{1,61} = 7.75$; $P = 0.007$), lower jaw length ($F_{1,61} = 4.59$; $P = 0.04$), the distance from the quadrate to the tip of the snout ($F_{1,61} = 5.35$; $P = 0.02$), snout length ($F_{1,61} = 7.00$; $P = 0.01$), and bite force ($F_{1,61} = 26.58$; $P < 0.001$).

TABLE 1. MORPHOMETRIC CHARACTERIZATION OF A NATIVE (LITTLE CAYMAN) AND INTRODUCED (CAYMAN BRAC) POPULATION OF *ANOLIS MAYNARDI*.

	Little Cayman		Cayman Brac	
	Male (n = 14)	Female (n = 13)	Male (n = 30)	Female (n = 9)
Snout-vent length (mm)	68.9 ± 3.1	51.3 ± 3.1	70.3 ± 3.5	50.6 ± 1.5
Body mass (g)	6.6 ± 0.9	2.5 ± 0.6	6.5 ± 1.1	2.8 ± 0.4
Head length (mm)	22.2 ± 1.2	15.3 ± 0.7	18.3 ± 2.0	14.6 ± 0.5
Head width (mm)	10.0 ± 0.6	6.9 ± 0.4	9.9 ± 0.6	6.7 ± 0.4
Head depth (mm)	7.1 ± 0.4	5.1 ± 0.4	7.3 ± 0.4	5.0 ± 0.2
Lower jaw length (mm)	23.8 ± 1.5	15.5 ± 0.9	24.2 ± 1.5	15.1 ± 0.5
Quadrate tip (mm)	21.7 ± 1.4	14.2 ± 0.9	22.0 ± 1.4	13.7 ± 0.5
Snout length (mm)	18.2 ± 1.2	12.0 ± 0.6	18.5 ± 1.1	11.6 ± 0.4
Open in-lever (mm)	2.2 ± 0.2	1.3 ± 0.4	2.2 ± 0.2	1.4 ± 0.1
Close in-lever (mm)	3.5 ± 0.3	2.2 ± 0.4	3.5 ± 0.3	2.1 ± 0.1
Bite force (N)	8.6 ± 1.6	3.5 ± 0.9	11.9 ± 2.5	4.0 ± 0.6
Body length (mm)	31.9 ± 1.7	25.2 ± 2.7	32.8 ± 1.9	25.5 ± 1.8
Body width (mm)	10.9 ± 0.9	7.6 ± 0.9	10.4 ± 1.1	7.2 ± 0.7
Body height (mm)	9.2 ± 0.7	6.4 ± 0.9	9.5 ± 0.8	7.0 ± 0.6
Femur length (mm)	13.0 ± 0.6	9.6 ± 0.7	13.2 ± 0.7	9.2 ± 0.4
Tibia length (mm)	13.0 ± 0.6	9.6 ± 0.7	13.7 ± 0.6	9.8 ± 0.3
Metatarsus length (mm)	8.2 ± 0.4	6.0 ± 0.4	8.4 ± 0.3	5.9 ± 0.2
Longest-toe hind limb (mm)	9.7 ± 0.6	7.4 ± 0.6	10.4 ± 0.4	7.3 ± 0.4
Hind-limb length (mm)	43.8 ± 1.8	32.6 ± 2.1	45.7 ± 1.7	32.2 ± 0.8
Humerus length (mm)	11.4 ± 0.8	8.1 ± 0.8	11.4 ± 0.7	8.0 ± 0.3
Radius length (mm)	9.4 ± 0.6	6.7 ± 0.5	9.7 ± 0.5	6.0 ± 1.0
Metacarpus length (mm)	3.6 ± 0.4	2.8 ± 0.3	3.6 ± 0.3	2.7 ± 0.3
Longest-toe forelimb (mm)	5.7 ± 0.4	4.1 ± 0.3	5.8 ± 0.4	3.9 ± 0.3
Forelimb length (mm)	30.2 ± 1.6	21.6 ± 1.6	30.5 ± 1.4	21.4 ± 0.7
Sprint speed (ms ⁻¹)			1.5 ± 0.3*	1.2 ± 0.2**

*n = 16; **n = 9. Table entries are means ± standard deviations.



Figure 1. A, Picture of an adult male *Anolis maynardi* from Little Cayman in its native evergreen shrubland habitat illustrating the greatly elongated rostrum. (B) Picture of a male *A. maynardi* in the sea grape habitat where it was very abundant on Little Cayman.

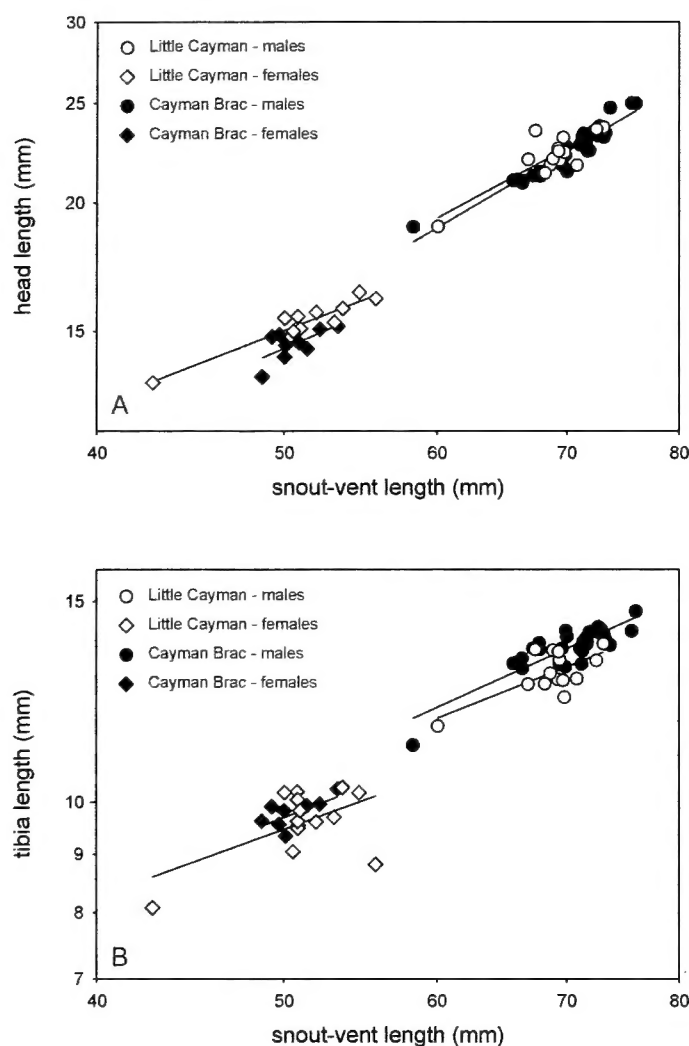


Figure 2. A, Differences in head dimensions between both populations and sexes of *Anolis maynardi*. Whereas in both populations males (circles) have longer heads than females (diamonds), animals from Little Cayman (open symbols) are characterized by longer heads for their body size compared with animals from Cayman Brac (filled symbols). B, Differences in limb dimensions between populations and sexes. Whereas males have longer tibia than females, animals from the introduced population on Cayman Brac have longer tibia than animals from Little Cayman.

Limb and body dimensions and sprint speed

Islands (Wilks' lambda = 0.48; $F_{15,47} = 3.40$; $P = 0.001$) and sexes (Wilks' lambda = 0.53; $F_{15,47} = 2.73$; $P = 0.004$) differed in limb dimensions, and the interaction between the two was also significant (Wilks' lambda = 0.61; $F_{15,47} = 2.04$; $P = 0.03$). Males had longer hind-limb dimensions than females: (for all hind-limb segments: $F_{1,61} > 11.00$; all

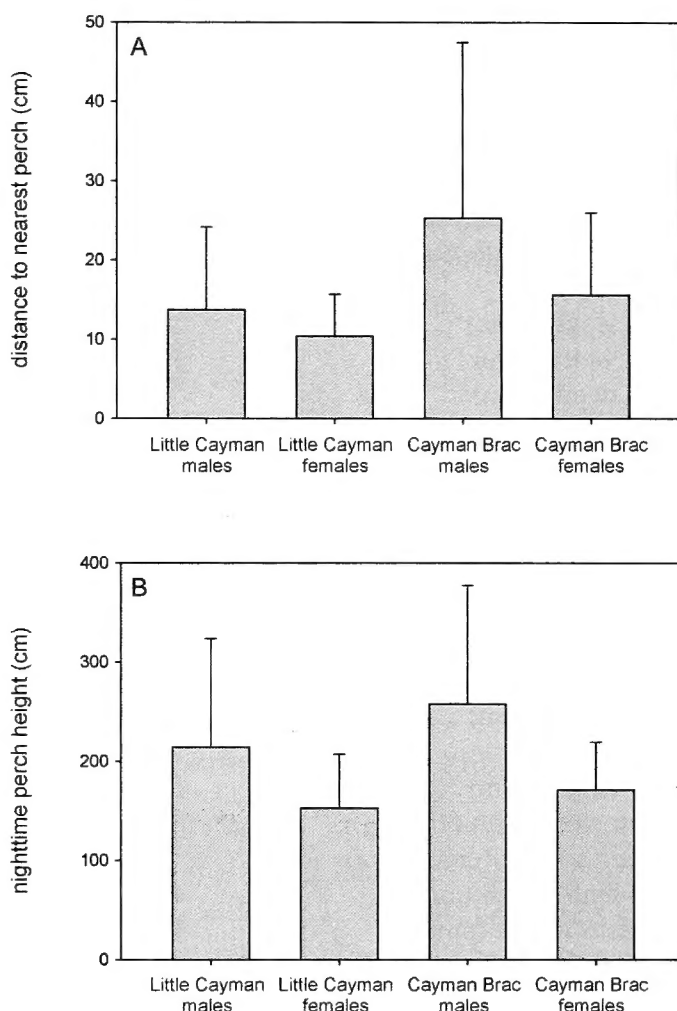


Figure 3. A, Differences in habitat use of *Anolis maynardi*. Animals on Cayman Brac use more open habitats characterized by greater distances to the nearest perch. B, Differences in sleep site use. Whereas in both populations males sleep higher than females, animals from the introduced population on Cayman Brac use higher vegetation than animals from Little Cayman.

$P < 0.01$) radius length ($F_{1,61} = 6.12$; $P = 0.02$), the length of the longest toe on the forelimb ($F_{1,61} = 10.28$; $P = 0.002$), and total forelimb length ($F_{1,61} = 11.34$; $P = 0.001$). Animals from Cayman Brac had taller but narrower bodies and longer tibia and radii than animals from Little Cayman: body height ($F_{1,61} = 6.55$; $P = 0.01$), body width ($F_{1,61} = 4.32$; $P = 0.04$), tibia length ($F_{1,61} = 8.44$; $P = 0.005$), and radius length ($F_{1,61} = 5.03$; $P = 0.03$) (Fig. 2; Table 1). Sex-by-population interaction effects were significant only for body height ($F_{1,61} = 5.23$; $P = 0.03$). Sprint speed was measured for animals

TABLE 2. HABITAT USE AND SLEEP SITE CHARACTERISTICS FOR A NATIVE AND AN INTRODUCED POPULATION OF *ANOLIS MAYNARDI*.

	Little Cayman		Cayman Brac	
	Male (<i>n</i> = 29)*	Female (<i>n</i> = 24)	Male (<i>n</i> = 29)	Female (<i>n</i> = 32)
Daytime perch height (cm)	163 ± 118	139 ± 87	218 ± 95	158 ± 75
Daytime perch diameter (cm)	4 ± 3	6 ± 6	8 ± 8	9 ± 23
Distance to nearest perch (cm)	14 ± 10	10 ± 5	25 ± 22	16 ± 10
Diameter of nearest perch (cm)	2 ± 2	2 ± 2	4 ± 9	3 ± 7
	<i>n</i> = 16	<i>n</i> = 20	<i>n</i> = 7	<i>n</i> = 10
Nighttime perch height (cm)	214 ± 110	153 ± 55	258 ± 119	171 ± 48
Nighttime perch diameter (cm)	5 ± 6	9 ± 6	1 ± 1	8 ± 15
	<i>n</i> = 22	<i>n</i> = 15	<i>n</i> = 24	<i>n</i> = 30
Body temperature (°C)	31.5 ± 1.7	32.0 ± 1.4	32.4 ± 2.0	33.0 ± 1.8
Air temperature (°C)	29.2 ± 2.4	30.5 ± 1.6	29.8 ± 2.2	30.5 ± 2.2

*Table entries are means ± standard deviations.

on Cayman Brac only and differs between the sexes ($F_{1,23} = 5.85$; $P = 0.02$), with males being faster than females.

Habitat use

Populations (Wilks' lambda = 0.90; $F_{4,96} = 2.54$; $P = 0.045$), but not sexes (Wilks' lambda = 1.08; $F_{8,192} = 1.08$; $P = 0.38$), were different in habitat use. The interaction between population and sex was also not significant (Wilks' lambda = 0.95; $F_{4,95} = 1.28$; $P = 0.28$). Populations differed in the distance to the nearest perch ($F_{1,99} = 8.27$; $P = 0.005$), with animals from Cayman Brac being characterized by a greater distance to the nearest perch than animals from Little Cayman (Fig. 2, Table 2). Sexes (Wilks' lambda = 0.86; $F_{2,61} = 4.92$; $P = 0.01$) and populations (Wilks' lambda = 0.88; $F_{2,61} = 4.34$; $P = 0.02$) also differed in their sleep sites. The interaction effect was, however, not significant (Wilks' lambda = 0.99; $F_{2,61} = 0.43$; $P = 0.65$). Differences between sexes and populations were significant for both perch height (sex: $F_{1,63} = 4.77$; $P = 0.03$; population: $F_{1,63} = 4.79$; $P = 0.03$) and perch diameter (sex: $F_{1,63} = 6.03$; $P = 0.02$; population: $F_{1,63} = 4.49$; $P = 0.04$), with

males sleeping higher but on narrower substrates than females and animals on little Cayman sleeping lower and on broader substrates than animals from Cayman Brac (Fig. 3; Table 2).

Temperature

Populations ($F_{1,85} = 5.47$; $P = 0.02$) but not sexes ($F_{1,85} = 2.33$; $P = 0.13$) differed significantly in body temperature, with animals from Cayman Brac having higher body temperatures on average than animals from Little Cayman (Table 2). This difference was, however, not a consequence of variation in air temperature as no differences were observed in air temperature between populations ($F_{1,85} = 0.46$; $P = 0.50$).

DISCUSSION

Anolis maynardi is a typical “green anole,” as trunk–crown species are often called. Rarely found on the ground, it uses a wide variety of arboreal habitats (only 15% of the animals were observed at a height lower than 1 m)—including trunks, narrow branches, twigs, and leaves—from eye level to the top of the canopy. Often locally abundant, the

species is found everywhere where appropriate vegetation—primarily trees or human structures—occurs.

Our surveys of animals on Little Cayman showed that they are relatively abundant and can be found throughout the island in a variety of vegetation types and habitats. However, animals were clearly most abundant in sea grape-dominated hemisclerophyllous evergreen shrubland along the southern edge of the island and in the relatively dense but low forest on the northern part of the island. Very few animals were observed in the mangroves. The wind-swept vegetation on the northeast coast of the island was also characterized by a lower abundance of individuals. On Cayman Brac animals were abundant in man-modified parkland near the airport and in the forested central part of the island.

Differences between sexes

Our data for both populations indicate a clear sexual dimorphism in body size, with males being larger than females (Grant 1940; Franz and Seidel, 1994). This has been observed for a closely related species, *Anolis carolinensis* (Irschick *et al.*, 2005), and is characteristic for trunk-crown anoles in general (Butler *et al.*, 2000). In addition to being dimorphic in body size, male *A. maynardi* also have relatively longer heads and snouts (Franz and Seidel, 1994) and have relatively longer hind limbs than females, patterns that are also exhibited by *A. carolinensis* (Irschick *et al.*, 2005). The wider and overall larger heads of males give them a performance advantage and consequently males have greater relative bite forces than females (Table 1). Finally, our data suggest that at least for the animals from Cayman Brac, males also have higher sprint speeds than females, which may be related to the intersexual difference in limb length (Macrini and Irschick, 1998).

Differences between populations

Lizards on the two islands differed in ecology, morphology, and performance. For example, individuals from Little Cayman have longer heads and snouts and lower bite forces. Although it remains unclear why individuals on Little Cayman have relatively lower bite forces despite their relatively wider heads, we suggest that subtle shape differences in the adductor chamber (e.g., see Herrel *et al.*, 2007) may lie at the base of this result. Beyond differences in head size and shape, our data suggest that animals from the introduced population on Cayman Brac also have relatively longer limbs. This accords well with the use of generally (but not significantly so) wider perches on Cayman Brac (Table 2), which is known to be correlated to the evolution of greater limb lengths in Greater Antillean anoles (Losos, 2009). The use of wider perches is reflective of the overall habitat structure on Cayman Brac, which is characterized by a more open, less densely forested habitat with larger and taller trees. Indeed, Cayman Brac's tilted, elevated plateau (where we caught the majority of the lizards included in our sample) is dominated by xeromorphic semi-deciduous forest. This is reflected in the significantly greater distance to nearest perch for animals on Cayman Brac compared with Little Cayman. As a result of the more open habitat structure on Cayman Brac, animals on that island are more exposed with less cover, which may explain why Cayman Brac lizards had higher body temperatures on average (but note that air temperatures did not differ between Cayman Brac and Little Cayman). However, our visit to Cayman Brac came only 5 months after the island was severely affected by Hurricane Paloma in November 2008. Paloma stripped the foliage off many trees and felled many others, opening up the canopy (Godbeer *et al.*,

2008). Consequently, the differences in habitat structure and attendant lizard ecology may have been a result of these differences and possibly may disappear as the vegetation on Cayman Brac recovers.

The morphological differences between *A. maynardi* on Little Cayman and Cayman Brac could have three explanations. First, the differences may represent rapid evolutionary adaptation to different environmental conditions experienced by the introduced population. Alternatively, second, the differences may represent phenotypic plasticity; anoles growing in different environments may develop different phenotypic characteristics. Although plasticity has not been much studied in anoles, laboratory experiments have shown that *A. carolinensis* and *Anolis sagrei* both develop longer hind limbs if they are raised on broader surfaces (Losos *et al.*, 2000; Kolbe and Losos, 2005). Finally, third, the Cayman Brac population may not have changed at all, but rather may be derived from a population on Little Cayman that we did not sample. If this is the case, it would indicate an interesting extent of geographic variation on a relatively small island like Little Cayman.

Much still remains to be learned about the biology of this little-known but fascinating species. The adaptive significance, if any, of the extraordinarily elongated snout of males of the species is unclear. Biomechanics of jaw movement suggest that long jaws would give an individual a performance advantage in capturing mobile, flying prey items (Herrel *et al.*, 2007). Why this trait is so dimorphic also requires explanation; sexual selection is one obvious possibility, with long snouts potentially benefitting males during male–male contests involving jaw locking. In addition, the impact of the introduction of *A. maynardi* on the native fauna of Cayman Brac also merits investigation, as well as the extent to which this species may be adapting to local conditions.

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